Many quantitative trait loci for feather growth in an F broiler × layer cross collocate with body weight loci

Many quantitative trait loci for feather growth in an F2 broiler X layer cross collocate with body weight loci

P.M. Hocking, D.M. Morrice, A.S. Law and D.W. Burt

The Roslin Institute and Royal (Dick) School of Veterinary Studies, University of Edinburgh, Easter Bush, Midlothian EH25 9RG, Scotland

Abstract

1. A genome-wide scan of 467 F2 progeny of a broiler x layer cross was conducted to identify quantitative trait loci (QTL) affecting the rate of growth of the tail, wing and back feathers, and the width of the breast feather tract, at three weeks of age.

2. Correlations between the traits ranged from 0□36 to 0□61. Males had longer tail and wing feathers and shorter back feathers than females. Breast feather tract width was greater in females than males.

3. QTL effects were generally additive and accounted for 11 to 45% of sex average feather lengths of the breeds, and 100% of the breast feather tract width. Positive and negative alleles were inherited from both lines, whereas the layer allele was larger than the broiler allele after adjusting for body weight.

4. A total of 4 genome-significant and 4 suggestive QTL were detected. At three or 6 weeks of age, 5 of the QTL were located in similar regions as QTL for body weight.

5. Analysis of a model with body weight at three weeks as a covariate identified 5 genome significant and 6 suggestive QTL, of which only two were coincident with body weight QTL. One QTL for feather length at 148cM on GGA1 was identified at a similar location in the unadjusted analysis.

6. The results suggest that the rate of feather growth is largely controlled by body weight QTL, and that QTL specific for feather growth also exist.

Introduction

Rapid feather growth is important in broiler chickens because slaughter at an early age is only possible if feathers are sufficiently mature to facilitate mechanical removal. Feathers also provide insulation, thereby reducing energy requirements, and may protect the skin against environmental insults from both the litter and other birds. Genetic variation for the rate of feather growth may exist in commercial lines, and this was investigated in an F_2 broiler layer cross by searching for quantitative trait loci (QTL) for feather growth in different areas of the body. It was also possible to assess the hypothesis that feather growth QTL were different from previously identified QTL for body weight in this cross (Sewalem et al., 2002).

As broilers become larger, the breast feather tract may stretch to accommodate the increasing mass of breast muscle and reduce the effective feather cover over this part of the body. Therefore, the width of the breast feather tract was measured in addition to breast feather length.

The primary objective of this research was to identify QTL for feather growth in major feather tracts (breast, back, wing and tail feather length) and breast tract width in a broiler□layer F_2 population at three weeks of age. It also reports comparable measures for the parent lines for comparison with the F_2.

Materials and Methods

Parent lines

In total, 40 day-old male and 40 female chicks were obtained from the Ross 308 male broiler line (Aviagen, Newbridge, Edinburgh) and from a White Leghorn layer line maintained at the Roslin Institute. The chicks were housed in 8 floor pens on wood shavings and fed ad libitum on a commercial layer chick starter diet. The broilers were vent-sexed at hatch, whereas the layers were sexed by a DNA method from a drop of blood obtained from the wing vein. At 14 d of age the birds were allocated to 16 pens (1.5 x 2.5 m) containing one sex of each breed in groups of 10. Feather measurements (see below) were made on 4 birds in each pen selected at random on the basis of wingband number.

Production of an F2 broiler\layer flock

Two males from a White Leghorn egg laying (L) line of chickens and the broiler (B) male line were each mated with a female from the other line to create $4F_1$ families. At 30 weeks of age, 8 male and 32 female F_1 were selected for breeding the F_2 generation in a balanced mating scheme. Over 500 F2 chicks from 5 hatches were reared in 20 floor pens and fed ad libitum on a broiler ration (13 MJ ME and 280 g crude protein/kg).

Observations

At three weeks of age the birds were weighed. The lengths of the mid-tail, 3rd primary (remige) and longest caudal back feather were measured with a ruler. The

width of the breast feather tract was also recorded. DNA was prepared by standard procedures from a 2 ml blood sample as described previously (Sewalem et al., 2002).

Genotyping

Genotyping was conducted using 123 microsatellite markers covering 24 autosomal linkage groups and the Z sex chromosome (Table 1) on the grandparents, F1 and F2 offspring. Pedigree, genotypes and traits were stored in the resSpecies database (Law and Archibald, 2000). The genetic linkage map was based on a map from the same population used in a previous analysis of health traits (Navarro et al., 2005). The map covered 2600 cM, excluding 8 chromosomes with single markers (Table 1).

Statistical analysis

The experiment to compare the parent lines was a completely randomised design. The data were analysed by a simple two way model of line x sex.

Means and standard errors for each trait in the F2 were computed by a generalised analysis of variance, with pen as a random effect, and family, sex and family x sex interactions as fixed effects. Phenotypic correlations between the feather traits and three week weight were determined in the F2.

Complete data from 467F2 individuals of 30 full sib families were available for analysis after edits. QTL analysis was performed using the least squares method of Haley and Knott (1992) for crosses of out-bred lines for the feather traits and body weight at three and 6 weeks of age. The initial genome scan was conducted of a model with additive and dominance effects using GRID-QTL, which produces an

exhaustive scan for marginal effect QTL with background effects for all other suggestive and significant QTL in an iterative scheme (Wei et al., 2007). This was followed by an analysis in QTL-Express (Seaton et al., 2002) of QTL□sex interactions for each QTL, including background genetic effects that were identified in the first stage. The statistical model included fixed effects for sex, family and pen; and the data were also analysed with a covariate for three week body weight. F-tests of statistical significance were based on 5000 replicates in GRID-QTL. QTL that achieved an F value exceeding the $P<0.10$ chromosome-wide threshold were considered to be suggestive.

Significance of QTL x sex interaction effects were based on conventional F values. QTL identified as suggestive or significant on the Z-chromosome in the initial analysis were reanalysed in QTL-Express with a simple additive model. The proportion of phenotypic variance explained by the QTL was estimated as the proportional difference (%) in the residual sum of squares from fitting the model, with and without the QTL.

The data for three and 6 week body weight were analysed using the same model and automated GRID-QTL procedures for comparison of the locations of body weight and feather trait QTL.

Results

Mean feather lengths, breast tract width and body weight at three weeks for both lines and sexes are presented in Table 2. Feathers were significantly longer, and breast feather tract was wider, in broilers compared with layer chickens ($P<0.01$), consistent with the 5-fold greater body weight of the broilers (Table 2). Broiler males

were significantly heavier than females, whereas body weight was similar in layer males and females at this age (line x sex interaction,(P <0.05). Differences in feather traits between males and females were generally not significant (Table 2).

There was no evidence for a family x sex interaction in the F2 data, and means for males and females for each trait are presented in Table 3. Males were heavier than females, had longer tail and wing feathers, shorter back feathers and wider breast feather tract than females (P <0□001). Phenotypic correlations between feather lengths are given in Table 4.

Correlations were moderately high between breast feather tract width and back feather length, and lower for tail and wing length. Correlations between body weight and feather traits ranged from 0□36 to 0□48 (Table 3).

There were marginally significant QTL□sex interactions for tail and back feather length on the Z chromosome, and for back feather length on chromosome 5, but these were eliminated when body weight was included as a covariate in the analysis. For clarity of presentation, these interactions were ignored and results of the QTL analyses for males and females combined are presented (Table 5).

Four genome-significant QTL for feather length were identified on Gallus gallus autosome 1 (GGA1), GGA7 and the sex chromosome Z (Table 5). Analysis of the model with body weight as a covariate provided evidence for 2 QTL on GGA1, a single QTL on each of GGA4 and GGA9, and a QTL for breast feather tract width on GGA4.

The magnitude of the dominance estimates for feather lengths were generally small and associated with large standard errors. The dominance effects for breast feather tract width were large and significant for the analysis without the covariate, but not for the model with body weight as a covariate (Table 5).

Genome significant QTL accounted for 1.6 to 6.0% of the phenotypic variation for feather length (Table 5), similar to other traits in this and other crosses (Hocking, 2005). The proportion of phenotypic variance explained by the sum of the QTL effects for body weight was 19.3% compared with 8.8, 2.5, 5.3 and 5.9% respectively for tail, wing and back feather lengths and feather tract width; corresponding proportions for the analysis with body weight as a covariate were 27.2, 4.1, 2.8 and 6.9%.

Discussion

QTL generally had additive effects, and the allele inherited from the White Leghorn had a greater effect than the alternative allele from the broiler male line on tail feather length, but not wing and back feather length, or breast tract width.

In contrast to these results, the additive effect of the layer allele was larger than the broiler allele in all but one of the QTL in the covariance analysis. The feather lengths in the White Leghorn were shorter in absolute terms but longer in relation to body weight than in the broilers. The apparent anomaly that layer QTL increased feather length in the cross, even though the layer feathers are shorter in absolute terms, may be a consequence of the permissive effect of growth factors from the broiler genotype increasing feather growth in the cross.

The additive effects of the feather length QTL were relatively small compared with the mean of the F2, being in the range 2.1 to 6.0% for the unadjusted analysis, and 1.7 to 7.7% for the analysis with body weight as a covariate. However, when expressed as a proportion of the line differences from Table 2, individual QTL account for 11 to 45% of the sex average feather lengths and at least 100% of the difference in breast

feather tract width. The results suggest that the study has identified a significant proportion of the genetic loci affecting the differences in feather growth between the lines.

Inspection of the QTL locations for feather traits, and QTL for bodyweight at three and 6 weeks that lie within 25cM (half the minimum 95% confidence interval) of these QTL, show that 5 of 8 feather trait QTL collocate with QTL for body weight at three weeks of age (Table 6). There were two genome-significant QTL (on GGA1 and GGA7) that were not associated with three week body weight QTL, but the QTL on GGA7 was not detected in the covariance analysis. Only the QTL on GGA1 at 145 or 148cM is therefore likely to be a purely feather length QTL. A QTL for breast tract width on GGA4 at 151cM was similar to the QTL for tail feather length at 153cM in the covariate analysis, and with QTL for body weight at three and 6 weeks of age (Table 6).

Podisi et al. (2011) and others have pointed out that including a genetically controlled and phenotypically correlated trait as a covariate in the analysis will affect the evidence for a QTL at a specific location, depending on the direction and magnitude of QTL effects on the two traits. The phenotypic correlation between the feather traits and body weight were generally low, accounting for less than 25% of the variation in the feather traits, and QTL for feather traits that do not collocate with body weight QTL after covariance analysis are probably not weight related. The covariance analysis identified QTL for tail feather length on GGA4, GGA9 and GGA15, and wing feather length on GGA1, and these are likely to be genuine feather length QTL. The QTL for breast tract width on GGA4 in both analyses collocate with large QTL for body weight on GGA4, and is undoubtedly a weightrelated trait. Breast tract width is important in providing feather cover to protect the breast skin from

damage, but this study has not identified a genome-wide significant QTL that would indicate that selection for a wider tract would be feasible.

The previous analysis of these data (Sewalem et al., 2002) identified several QTL that were not found in the present analysis and vice versa. There were more markers on GGA1 and GGA4 in the present analysis that may explain part of these differences, but the absence of evidence for a QTL on GGA7 for three week weight, and on GGA2, GGA7 and GGA8 for body weight at 6 weeks in this study is surprising, and a cause of some concern. Leaving aside the possibility of errors in the analysis, one explanation is that the automated and exhaustive analysis performed by GRID-QTL is more efficient and accurate than the piecemeal manual analysis using the earlier QTL-Express software.

To the authors' knowledge there are no comparable publications on the identification of QTL for feather growth. Reports of QTL for feather pecking, based on microsatellite association mapping, provide no evidence for QTL that overlap with the QTL for feather growth found in this study (Buitenhuis et al., 2003a,b; Keeling et al., 2004; Jensen et al., 2005). A large study of feather condition score in several lines of chicks, using over 1000 SNP markers biased towards genes that control behaviour or immunity, revealed significant associations on GGA4 and GGA7 that are similar to the locations on these chromosomes reported here. It is not clear why genes for feather growth and feather pecking should be linked, and the general lack of association of all the suggestive and significant relationships with those reported in the literature suggests that this conclusion is correct.

The results of this study indicate that many QTL for body weight also affect feather growth, and that QTL for feather growth that are not related to body weight also exist.

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Tab.1

The number of microsatellite markers, first and last marker and map length on each chromosome in the QTL analysis

Chromosome	Number	First marker	Last marker	Map length (cM
1	25	LEI0146	MCW0107	552
2	12	LEI0163	MCW0157	474
3	11	ADLO131	MCW0040	308
4	27	ADL0143	LEI0073	241
5	6	LEI0082	ADL0298	166
6	4	ROS0062	ADL0323	88
7	3	LEI0064	ADL0180	129
8	2	ADL0179	ROS0075	94
9	4	ROS0078	MCW0134	132
10	1	ADL0209	–	–
11	5	MCW0097	ROS00112	71
12	2	ADL0240	ADL0044	33
13	3	MCW0340	ADL0225	70
14	1	MCW0123	–	–
15	2	LEI0083	MCW0080	45
17	1	ADL0199	–	–
18	2	ROS0022	ROS0027	23
22	1	ROS0073	–	–
23	2	MCW0249	ADL0289	8
24	1	ROS0113	–	–
26	1	ADL0285	–	–
27	1	ROS0071	–	–
28	2	ROS0095	ADL0299	39
32	1	ROS0102	–	–
Z	3	ROS0072	LEI0075	127
Total	123			2600

Tab.2

Means and standard errors of differences (SED) for tail, wing and back feather lengths, breast feather tract width, and body weight at three weeks of age in male and female chicks of a broiler male line and a White Leghorn layer line of chickens

Trait	Sex	Line		SED	Significance[1]		
		Broiler	Layer		Line	Sex	Interaction
Tail feather length, mm	M	53	38	4·6	**	ns	ns
	F	55	48				
Wing feather length, mm	M	88	75	2·4	***	ns	ns
	F	89	81				
Back feather length, mm	M	34	27	2·4	***	*	ns
	F	42	29				
Breast feather tract width, mm	M	11	5	0·7	***	ns	ns
	F	11	6				
Body weight, kg	M	1·14	0·22	0·025	***	**	*
	F	1·03	0·21				

[1] ***¼P <0.001; *¼P<0.05; ns¼not significant.

Tab.3

Means and standard errors of differences (SED) between male and female chicks of an F2 broiler layer cross at three weeks of age for tail, wing and back feather lengths, breast feather tract width, and body weight

Trait	Mean		SED	Significance[1]
	Male	Female		
Tail feather length, mm	59·0	56·6	0·62	***
Wing feather length, mm	96·3	94·2	0·52	***
Back feather length, mm	32·3	35·5	0·47	***
Breast feather tract width, mm	34·2	43·0	0·83	***
Body weight, g	439	409	5·6	***

[1] ***¼P <0.001.

Tab.4

Phenotypic correlations between tail, wing and back feather lengths, breast feather tract width and body weight at three weeks of age in male and female chicks of an F2 broiler layer cross. All correlations were significant (P<0.001)

Trait	Tail	Wing	Back	Tract
Tail feather length, mm				
Wing feather length, mm	0·61			
Back feather length, mm	0·60	0·60		
Breast feather tract width, mm	0·42	0·45	0·76	
Body weight, g	0·48	0·47	0·44	0·36

Tab.5

Location of QTL and estimates of additive (a) and dominance (d) effects for tail feather length, wing feather length and breast feather tract width at three weeks of age in an F2 broiler x layer cross. Each trait was analysed with and without body weight as a covariate

Trait	LG[1]	F[2]		LN[3]	a	d	VP%[4]
Feather traits with no covariate							
Tail feather length, mm	1	9·20	*	145	−1·93 ± 0·50	0·06 ± 0·82	3·7
	13	6·72	†	60	−1·67 ± 0·46	0·01 ± 0·69	2·6
	Z	10·37	**	127	1·22 ± 0·38	-	2·5
Wing feather length, mm	7	6·45	*	69	2·24 ± 0·62	0·64 ± 1·61	2·6
Back feather length, mm	13	7·43	†	45	1·62 ± 0·43	−1·08 ± 0·90	2·9
	Z	9·75	**	124	0·96 ± 0·31	-	2·4
Breast tract width, mm	4	8·48	†	151	1·92 ± 0·61	2·96 ± 1·02	3·4
	7	6·37	†	77	2·33 ± 0·85	−4·24 ± 1·92	2·5
Feather traits with body weight covariate							
Tail feather length, mm	1	21·43	**	148	−2·67 ± 0·41	0·13 ± 0·79	7·7
	1	5·18	†	295	−1·46 ± 0·46	−0·05 ± 0·90	1·6
	4	7·58	†	2	−0·99 ± 0·34	1·23 ± 0·51	2·5
	4	13·86	**	153	−2·05 ± 0·34	0·86 ± 0·66	4·8
	9	6·49	†	22	0·99 ± 0·34	1·23 ± 0·51	2·5
	9	17·03	**	60	−2·66 ± 0·46	0·24 ± 0·60	6·0
	15	6·70	†	31	−1·77 ± 0·55	2·21 ± 1·10	2·1
Wing feather length, mm	1	9·70	*	185	−1·08 ± 0·31	−1·20 ± 0·44	4·0
Back feather length, mm	3	7·01	†	134	−0·99 ± 0·31	−1·04 ± 0·53	2·8
Breast tract width, mm	3	8·66	†	168	−2·99 ± 0·83	−3·33 ± 2·23	3·0
	4	9·50	*	241	−2·01 ± 0·46	0·23 ± 0·65	3·9

[1] Linkage group (chromosome).

[2] F-ratio; **=P <0.01; * =P<0.05; † = suggestive.

[3] Location (cM) on the identified linkage group (chromosome).

[4] Proportion of total variance associated with the model.

Tab.6

Location of QTL for tail, wing and back feather length, and breast feather tract width with no covariate for body weight at three weeks, and QTL for body weight at three and 6 weeks of age in an F2 broiler x layer cross

Trait	LG[1]	Location of feather QTL, cM	Location of weight QTL, cM	
			3 weeks	6 weeks
Tail feather length, mm	1	145*	-	-
	13	60†	48†	60**
	Z	127**	127**	-
Wing feather length, mm	7	69*	-	-
Back feather length, mm	13	45†	48†	60**
	Z	124**	127**	-
Breast tract width, mm	4	151†	141**	129**
	7	77†	-	-

[1] Linkage group (chromosome).